

Diving behaviour of chinstrap penguins at Seal Island

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Abstract: Diving behaviour of chinstrap penguins (*Pygoscelis antarctica*) was studied in four adults brooding chicks on Seal Island, South Shetland Islands, Antarctica. During foraging trips to sea, chinstrap penguins made shallow, short duration dives almost continuously, for the most part within 50 m of the surface. Diving effort was concentrated during the daylight hours (10h00–15h00), although a second peak in effort was seen around midnight (22h00–02h00). These peaks were possibly due to the constraints of visual location of prey, chick provisioning, or the need to take advantage of diurnal changes in krill swarm densities or behaviour. It was estimated that most effort was concentrated 3–20 km from shore. Dive depth and duration averaged 31.0 m (± 26.3 m) and 72 s (± 36 s), respectively. Maximum dive depth and duration were 121 m and 180 s, respectively.

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Introduction

Much interest has recently been focused on the diving behaviour of penguins. Descriptions of diving depths have been published for emperor (*Aptenodytes forsteri*) (Kooyman & Croll 1987), king (*Aptenodytes patagonica*) (Kooyman *et al.* 1992, Kooyman *et al.* 1982), gentoo (*Pygoscelis papua*) (Croxall *et al.* 1988), chinstrap (*Pygoscelis antarctica*) (Lishman & Croxall 1983), Adélie (*Pygoscelis adeliae*) (Wilson *et al.* 1991, Naito *et al.* 1990, Whitehead 1989), macaroni (*Eudyptes chrysolophus*) (Croxall *et al.* 1988), and jackass (*Spheniscus demersus*) (Wilson 1985) penguins. With the exception of the studies by Wilson (1985), Whitehead (1989), Naito *et al.* (1990), and Kooyman *et al.* (1992), most researchers used dive histogram recorders, which record the number of dives to discrete depth increments. Foraging effort was found to be concentrated at specific depths, consistent with the distribution of prey species (reviewed by Croxall & Lishman 1987). In two studies (Lishman & Croxall 1983, and Croxall *et al.* 1988) it was hypothesized that foraging effort may be concentrated at night when prey are available closer to the surface as they migrate as part of the deep scattering layer. However, a lack of temporal information on diving effort has precluded confirmation of this hypothesis.

Less information has been available concerning the profile and duration of penguin dives and the timing of foraging effort. Trivelpiece *et al.* (1986) used radiotelemetry to measure dive durations and foraging range in sympatrically breeding gentoo and chinstrap penguins and found that the former dived for longer periods of time and spent a greater proportion of their foraging trip diving than did chinstrap penguins. Recently, smaller dive recorders have been developed allowing the measurement of the timing, duration, and depth of dives made by emperor penguins (Kooyman & Croll 1987), king penguins (Kooyman *et al.* 1992), Adélie penguins (Naito *et al.* 1990), gentoo penguins (Williams *et al.*

1992), and thick-billed murres (*Uria lomvia*) (Croll *et al.* 1992). These studies and similar research on pinnipeds have shown that diving depth and duration are closely correlated, dives often occur in discrete bouts, and diving depth and effort often show distinct diurnal patterns (see Kooyman 1989 for a review).

Because chinstrap penguins feed almost exclusively upon Antarctic krill (*Euphausia superba*) during the breeding season (Croxall & Furse 1980, Volkman *et al.* 1980), it is likely that penguin dive behaviour is strongly influenced by krill distribution and behaviour. Although studies of the horizontal and vertical distribution of krill have shown that these patterns may vary widely between seasons and locations (reviewed in Miller & Hampton 1989), some general patterns have been described for specific areas such as South Georgia: 1) krill swarms have been shown to migrate toward the surface (Croxall *et al.* 1985), and 2) become more dispersed at night (Everson 1982). Lishman & Croxall (1983) speculated that chinstrap penguins may take advantage of this migration, and adjust their diving behaviour accordingly. Using data obtained from time-depth recorders (TDRs), we report here the diving behaviour and timing of foraging of chinstrap penguins breeding on Seal Island, South Shetland Islands, and relate this to information on the distribution and behaviour of krill.

Materials and methods

Time-depth recorders were deployed on four adult chinstrap penguins, each with two chicks (1–4 weeks old being guarded by at least one adult at all times), on Seal Island, South Shetland Islands, Antarctica (60°59.5'S, 55°24.5'W) during January 1988. Mark IV microprocessor time-depth recorders (TDRs) (Wildlife Computers, Woodinville, WA, USA¹) with a data storage capacity of 64k bytes were used for data collection. The recorders weighed 107 g, measured 36 mm

Table I. Summary statistics for foraging dives (dives ≥ 5 m in depth or ≥ 20 seconds in duration) made by chinstrap penguins at Seal Island, South Shetland Islands, January 1988. Numbers in parentheses indicate standard deviations.

Bird. no.	No. trips	Mean trip length (h)	No. dives	Time first dive* (min)	Depth		Duration		Time at sea (h)	Time ashore (h)
					mean (m)	max (m)	mean (s)	max (s)		
1	20	11.6 (3.6)	3150	47.9 (25.7)	32.4 (23.2)	113	72.0 (32.4)	180	243.6	279.5
2	14	9.3 (3.8)	2163	27.6 (16.7)	34.0 (30.2)	121	72.0 (36.0)	180	130.7	213.4
3	20	13.3 (4.7)	2489	24.8 (20.3)	26.6 (25.1)	120	72.0 (39.6)	168	265.5	260.2
4	15	11.8 (6.4)	2723	78.0 (50.1)	30.9 (27.0)	112	66 (36.0)	138	176.9	225.2
Overall	69	11.0 (4.7)	10525	41.8 (38.1)	31.0 (26.3)	121	72 (36.0)	180	816.7	978.3

*Time elapsed from leaving the colony to first foraging dive.

wide x 22 mm high x 110 mm long, and were tapered anteriorly to reduce drag. Minimum depth resolution was ± 1 m, and depth was sampled every 10 s. TDRs were attached to the feathers of the middle of the back using a quick-setting adhesive (Devcon 5-minute epoxy) and two plastic cable ties. A conductivity switch on the TDR allowed the measurement of time spent on shore. After 2–3 weeks, the recorders were

recovered from the birds and the data were downloaded to a lap top computer via an RS232C serial port.

Results

A total of 12 023 dives was recorded for the four penguins between 9–31 January (Table I, Fig. 1). Two types of dive

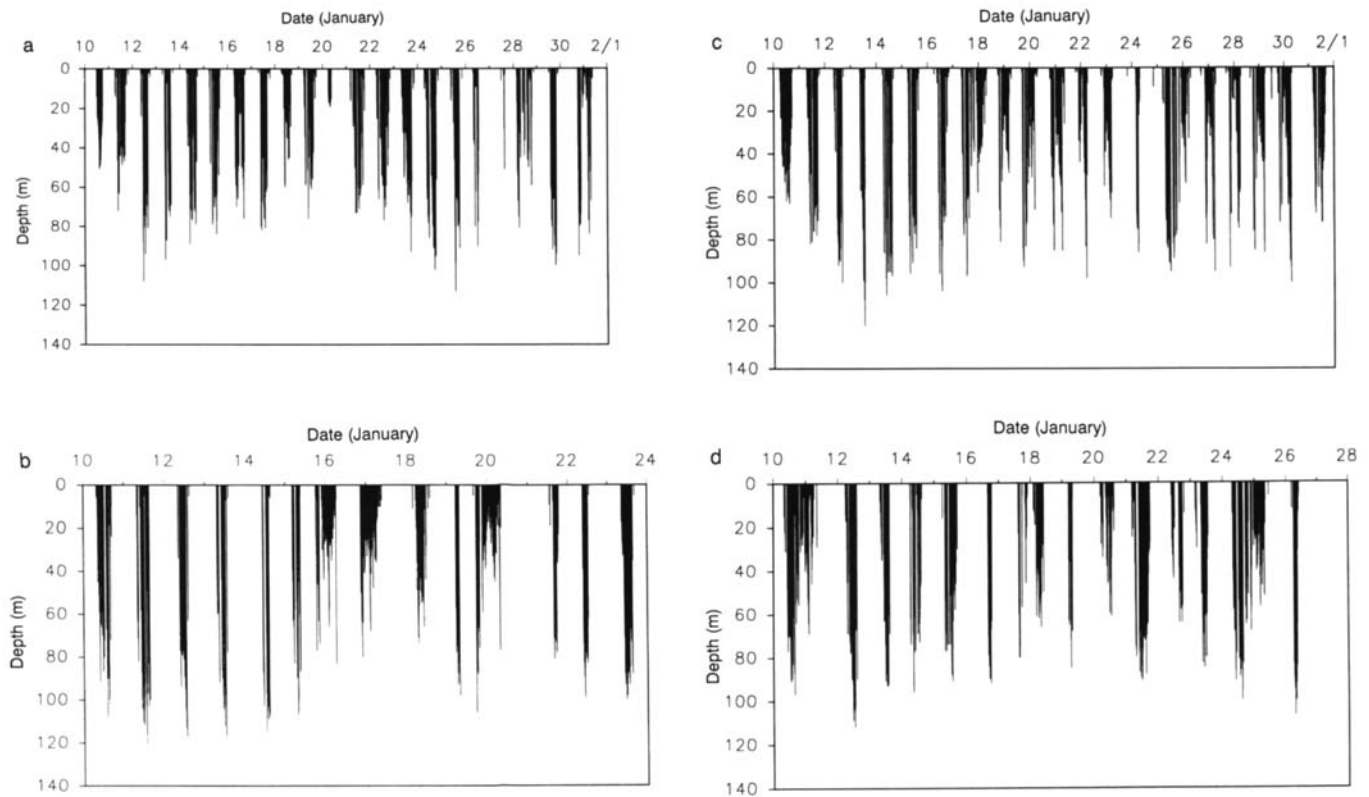


Fig. 1 a-d. Individual plots of diving activity (all dives) of chinstrap penguins at Seal Island, 1988. Vertical lines correspond to individual dives. Plots **a** through **d** correspond to chinstrap penguins 1 through 4.

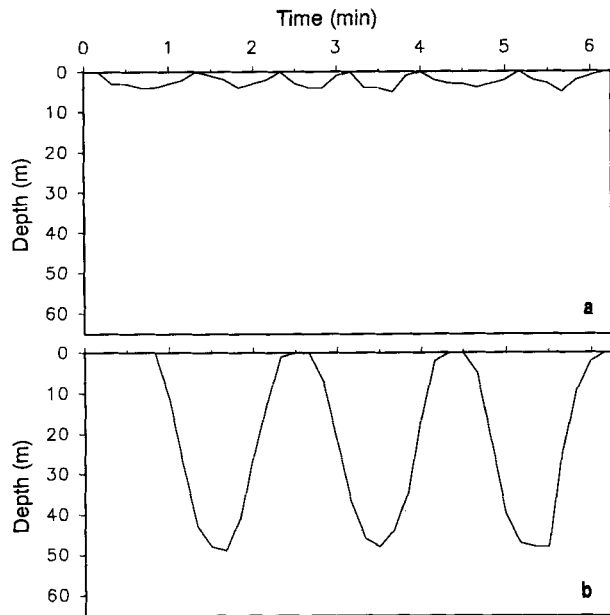


Fig. 2. a. typical porpoising/travelling dive pattern of chinstrap penguins. b. typical foraging dive pattern of chinstrap penguins. Data are from chinstrap penguin 1.

profiles were typically observed: 1) shallow, short duration dives probably associated with near-surface travelling and porpoising behaviour (Fig. 2a), and 2) deeper, longer duration, U-shaped dives presumed to be associated with feeding (Fig. 2b). The distribution of dive characteristics showed these two dive types as two distinct peaks in depth and duration (Fig. 3). Therefore, for this study we considered dives less than 5 m in depth and 20 s in duration as porpoising/travelling dives. These shallow, short duration porpoising/travelling dives ($n=1498$) averaged (mean \pm s.d.) 2.3 ± 0.56 m in depth and 10 s in duration (Fig. 4); they were excluded from subsequent analyses of foraging behaviour. Dives with a maximum dive depth ≥ 5 m or duration ≥ 20 s were considered foraging dives.

The number of foraging dives totaled 10 525 during 69 trips to sea (Fig. 5), giving a mean of 153 foraging dives per foraging trip. Analysis of variance showed that neither the maximum dive depths ($F=1.32$, $df=3$, $P>0.05$) nor durations of individuals' dives (ANOVA $F=2.38$, $df=3$, $P>0.05$) were significantly different, so the records of the four individuals could be pooled for further analyses.

The maximum depth per dive averaged 31.0 ± 26.3 m while dive duration averaged 72.0 ± 36.0 s. The maximum dive depth and duration recorded for all birds were 121 m and 180 s, respectively. Most foraging dives made by the penguins were shallow, less than 20 m in depth (Fig. 6), whilst dive duration was evenly distributed between 10 and 110 s (Fig. 7). Few foraging dives were greater than 60 m and 110 s. Dive duration and depth were highly correlated (duration = $36.8 + 1.2$

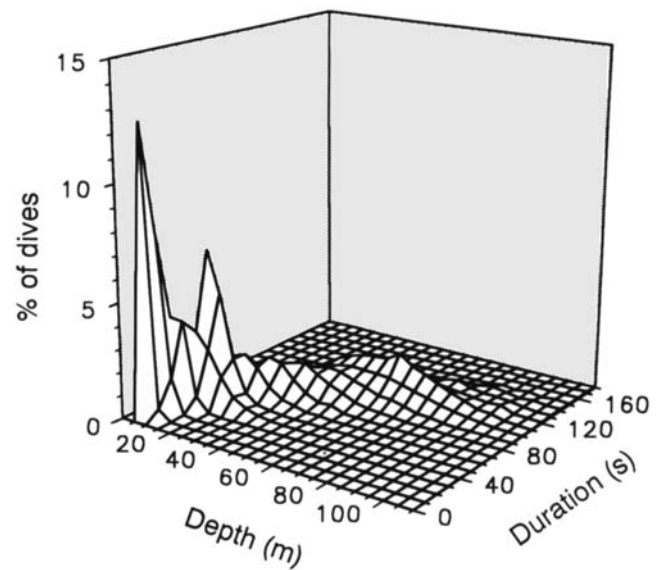


Fig. 3. Frequency distribution by depth and duration of all dives made by four chinstrap penguins. $n=12023$ dives.

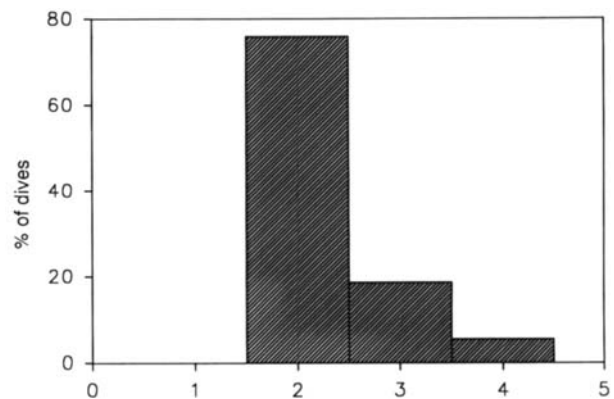


Fig. 4. Frequency distribution of depth of all porpoising/travelling dives (dives <5 m and <20 s in depth and duration) made by chinstrap penguins. $n=1498$ dives.

depth, $r^2=0.96$) (Fig. 8); however dive duration tended to level off at around 130 s for dives deeper than 80 m.

Diving effort was concentrated at noon and midnight (Fig. 9), with dive depths averaging 45 m between 10h00 and 14h00, and 22 m between 22h00 and 02h00 (Fig. 10). Plots of the dive record for each bird are shown in Fig. 1; diving data are summarized in Table I. The four birds tended to dive around noon or midnight on any given day, with the focus of single trips centred around one of these times. This pattern would often reverse: it was not uncommon for a bird that had been diving during daytime trips to sea for several days to subsequently switch to night diving. Such a switch would

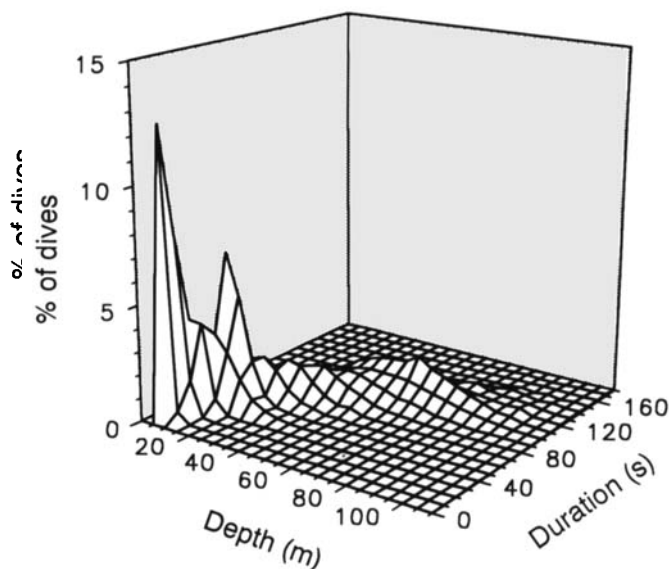


Fig. 5. Frequency distribution by depth and duration of foraging dives (dives ≥ 5 m or ≥ 20 s in depth and duration) made by four chinstrap penguins. $n=10525$ dives.

usually occur when a penguin remained at sea for an extended trip, diving throughout the day and continuing into the night. While at sea, the birds dived almost continuously, rarely pausing for more than five minutes between dives. Foraging trip duration for all trips combined averaged 11.0 ± 4.7 h.

Discussion

Effect of recorder

The potential effects of attached dive recorders on the behaviour of birds have been discussed (Wilson *et al.* 1986, Cairns *et al.* 1987, Croxall *et al.* 1988, Croll *et al.* 1991, Croll *et al.* 1992,

Kooyman *et al.* 1992). Attached devices, through the effects of drag or the discomfort of attachment, may affect the behaviour and energetic requirements of the bird. Wilson *et al.* (1989a) found that foraging trip duration and nest desertion increased in Adélie penguins after 19 days of recorder attachment. The recorders used in the present study had a frontal cross-sectional area of 7.92 cm^2 , causing a 5.3% increase in frontal cross-sectional area for a swimming penguin of $c. 150 \text{ cm}^2$ (Croll *et al.* 1991). Using the equation of Wilson *et al.* (1986) to predict the effect of an attached device on swimming speed, a 5.3% increase in frontal cross-sectional area should result in a 15% reduction in swimming speed, which could lead to an increase in foraging trip duration and a reduction in diving efficiency (leading to shorter duration or shallower dives). However, it should also be noted that, in contrast to the flat-ended devices used by Wilson *et al.* (1986), we used TDRs with tapered fronts to reduce drag. Croll *et al.* (1991) found no significant increase in foraging trip duration in chinstrap penguins equipped with TDRs identical to those used in the present study. The mean foraging trip durations of penguins in the present study (11 h) were similar to those reported by Croll *et al.* (1991) for unencumbered penguins on Seal Island in 1989/90 (9.3 h). Although the penguins in this study appeared to behave normally following instrument attachment, these potential effects should be kept in mind.

Foraging vs. travelling dives

It is important to distinguish between dives that are associated with travelling to and from feeding areas and dives that are associated with foraging. The inclusion of travelling dives as part of the feeding effort will tend to overestimate foraging effort, while foraging dives that are mistakenly excluded from analysis as travelling dives will lead to underestimated effort. In the present study we have excluded dives less than 5 m in depth and less than 20 s in duration as likely travelling dives.

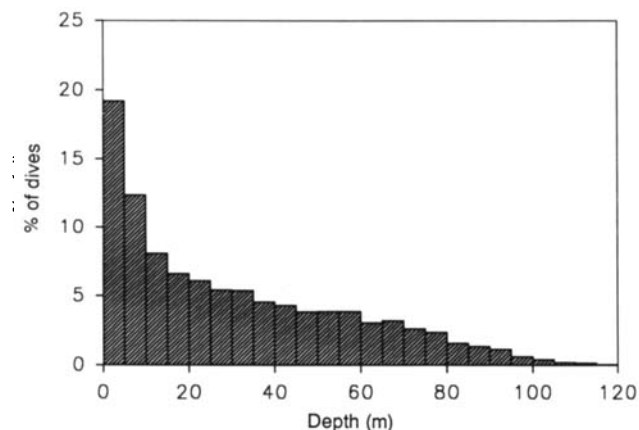


Fig. 6. Frequency distribution of depth of foraging dives (dives ≥ 5 m or ≥ 20 s in depth and duration) made by chinstrap penguins. $n=10525$ dives.

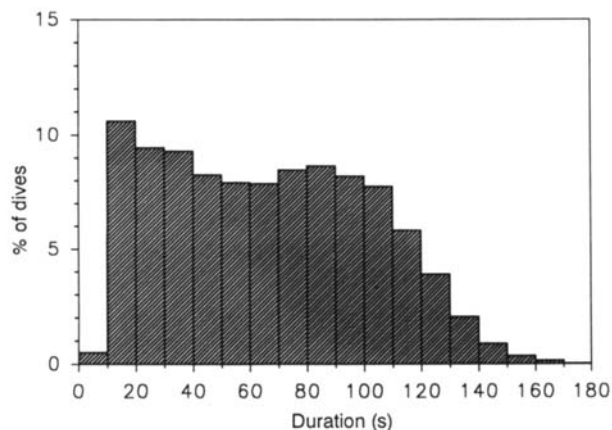


Fig. 7. Frequency distribution of duration of foraging dives (dives ≥ 5 m or ≥ 20 s in depth and duration) made by four chinstrap penguins. $n=10525$ dives.

These travelling dives averaged 2.3 m (± 0.56 m), and most of them (78%) were 2 m in depth (Fig. 4). Whereas Trivelpiece *et al.* (1986) found that chinstrap penguin porpoising and travelling dives averaged 50 s (determined by radio tracking), we believe that we have been conservative in excluding dives as travelling on the basis of < 20 s duration. Furthermore, chinstrap penguins were commonly observed porpoising away from the Seal Island colony to feeding areas offshore. The average dive depth and duration during the first 20 min of the foraging trips of the four penguins in the present study averaged 3.9 m (± 3.3 m) and 18.9 s (± 10.5 s) ($n=26$), respectively. Thus, we feel that our criterion for excluding dives < 5 m and < 20 s in depth and duration is a realistic means of differentiating between travelling and foraging dives.

Diving patterns

The dive records from Seal Island showed similarities and differences to the dive patterns observed for chinstrap penguins at other sites. The average duration of foraging dives (72 s) was less than that observed by Trivelpiece *et al.* (1986) at King George Island (91 s). The decreased mean duration may have been due to: 1) differences in the birds' behaviour, 2) the inclusion of some shorter duration dives near Seal Island which may not have been foraging dives, or 3) an overestimate of the dive durations near King George Island because of the method of measuring duration (reception of radio transmitter signals after the bird's back is completely out of the water). Foraging trip durations of penguins guarding chicks at Seal Island (11 h) were similar to those reported for TDR-equipped birds in 1989/90 on Seal Island (11.2 h), and slightly longer than those reported for unencumbered penguins on Seal Island (9.3 h) (Croll *et al.* 1991). However, these durations were shorter than those reported for chinstrap penguins guarding chicks at King George Island (16.7 h) and penguins feeding crèched chicks at Signy Island (33 h) (Lishman & Croxall 1983), but longer than those reported for the same species feeding crèched chicks at King George Island (5.3 h) (Trivelpiece *et al.* 1986). Chinstrap adults in the present study delivered an average of 2.2 feeds d^{-1} to their chicks compared to rates of 1.4 feeds d^{-1} and 0.7 feeds d^{-1} at King George Island and Signy Island, respectively. Thus, it appears that there is a high degree of geographical variability in chick provisioning rates during the guard stage. However, these differences may also reflect interannual differences in prey availability. The mean maximum diving depths were shallower for Seal Island penguins when compared to those measured near Signy Island (Lishman & Croxall 1983). Since the chinstrap penguins in all of these studies fed almost exclusively upon krill, differences in trip duration and diving depth probably resulted from temporal and spatial differences in prey availability rather than prey type.

The deepest dive recorded at Seal Island (121 m) is considerably deeper than the maximum of 70 m measured by Lishman & Croxall (1983) at Signy Island and is the deepest

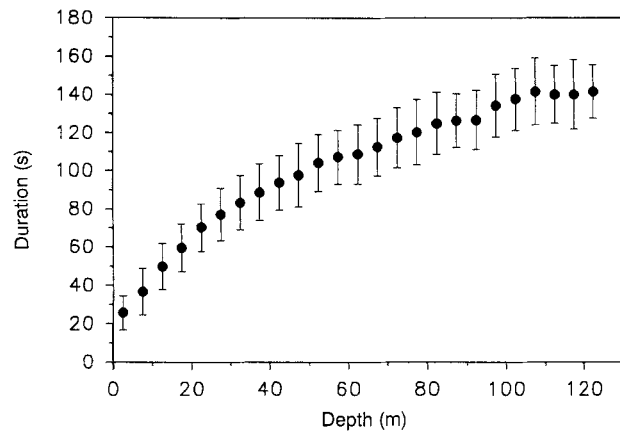


Fig. 8. Relationship of foraging dive (dives ≥ 5 m or ≥ 20 s in depth and duration) depth and duration of chinstrap penguins. Error bars indicate standard deviation. $n=10525$ dives.

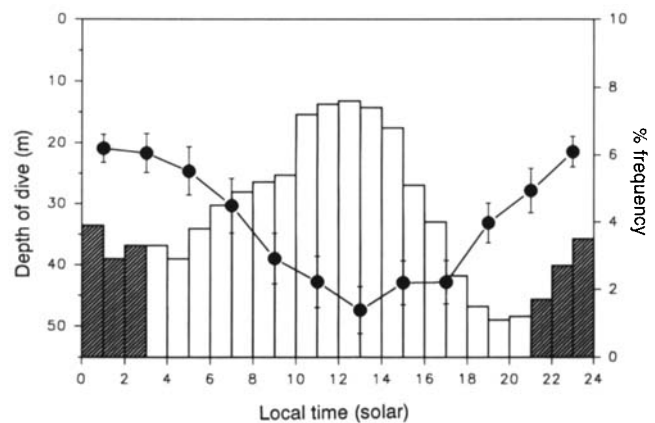


Fig. 9. Average (\pm s.d.) dive depth (solid circles) and frequency of foraging dives (histogram) by time of day for foraging dives of four chinstrap penguins. Foraging dives (dives ≥ 5 m or ≥ 20 s in depth and duration) are plotted. Darkened bars indicate hours of darkness at Seal Island. $n=10525$ dives.

thus far recorded for a pygoscelid penguin. However, king and emperor penguins have been measured diving to 304 and 265 m, respectively (Kooyman 1989, Kooyman *et al.* 1992) and the maximum dive depths of common and thick-billed murre (*Uria* spp.) have been measured to 180 and 210 m, respectively (Piatt & Nettleship 1985, Croll *et al.* 1992). The maximum dive duration measured at Seal Island (180 seconds) is only 40% greater than the average dive duration of 128 s measured for gentoo penguins (Trivelpiece *et al.* 1986). Compared to other deep-diving seabirds, chinstrap penguins at Seal Island are relatively shallow, short duration divers.

Diving in relation to krill behaviour

Several important aspects of krill behaviour may influence penguin foraging behaviour: 1) krill tend to occur in the upper

150 m of the water column (Miller & Hampton 1989); 2) krill have been shown to undergo a diel vertical migration in a number of studies (Croxall *et al.* 1985, Godlewska & Klusek 1987, Hampton 1985, Kalinowski & Witek 1980, Loeb & Shulenburg 1987), but not all individuals necessarily migrate, and this pattern is variable at different locations (Miller & Hampton 1989); and 3) Everson (1982) found that krill may also undergo a diel pattern of dense swarming in the daytime and a dispersion after dark.

Overall, 75% of chinstrap foraging effort on Seal Island was concentrated in water ≤ 50 m (Fig. 5). Diving effort was concentrated during the day, between 10h00 and 15h00 (Fig. 6), and diving depths at that time were deeper (40 m) than those observed during the evening (20 m) (Fig. 7). Two of the several non-exclusive possibilities that may explain this pattern are: 1) chinstrap penguins may rely principally on visual cues to capture prey, thus daylight feeding may be more efficient than night feeding when low light levels or the need to use the bioluminescence of their prey may make locating and capturing prey more difficult, 2) diel changes in krill behaviour, for example, diel changes in the depth or density of swarms, and/or the behaviour of krill (e.g. predator avoidance or feeding) may lead to a higher capture success rate during the day. However, as noted by Wilson *et al.* (1991), in view of the highly variable nature of krill distribution, generalizations of the feeding behaviour of penguins in relation to krill behaviour should be made with caution.

Antarctic fur seals (*Arctocephalus gazella*) showed a similar pattern of deeper dives during the daylight hours at South Georgia (Croxall *et al.* 1985). However, in contrast to our observations of chinstraps, fur seal diving effort at South Georgia was concentrated during the evening hours. One possible explanation for this difference may be that prey can more easily elude capture from fur seals than penguins during the day. Bengtson & Stewart (1992) suggested that the night time feeding behaviour of crabeater seals (*Lobodon carcinophagus*) was influenced by the predator avoidance behaviour of krill during daylight hours.

Wilson *et al.* (1989b) suggested that diel patterns in foraging trips of Adélie penguins were due to the birds' inability to locate prey during the evening rather than diurnal cycles in prey availability. Evidence from our TDR records do not support this hypothesis for chinstraps. Although prey capture may be facilitated during the day, diving effort does, nevertheless, continue in the evening. Approximately 15% of the dives made by chinstrap penguins were between 22h00 and 02h00, a period of darkness on Seal Island in January. Tomo (1983) reported that krill shoals several metres below the surface can be easily observed by their luminescence which may be used by chinstraps to visually locate them during the evening.

Foraging range

Stahel *et al.* (1985) using foraging trip duration and swimming speed of penguins to calculate a maximum foraging range. Wilson *et al.* (1989c) suggested that while these estimates provide a maximum range, assuming the bird did no diving or foraging, a more useful estimate of where the birds are actually foraging may be made by incorporating behavioural information. Kooyman *et al.* (1992) used the time elapsed from when the penguin leaves the colony to the time it makes its first foraging dive and an estimate of average swimming speed to calculate foraging distance in king penguins. Assuming a straight line path from the colony, a mean time to the first foraging dive of 41.8 min, a mean foraging trip duration of 11 h (Table I) and an average swimming velocity of 4.8 km h^{-1} (Trivelpiece *et al.* 1986), we estimate the minimum foraging distance from Seal Island for chinstrap penguins was 3.3 km, and the mean maximum was 26.4 km. Trivelpiece *et al.* (1986) calculated the maximum foraging range of chinstrap penguins on King George Island as 33 km using trip duration and swimming speed, while Wilson *et al.* (1989c) calculated the maximum foraging range adjusted for vertical distance covered in dives for this species breeding on Anvers Island as 3 km.

Although minimum and maximum foraging distance can be estimated from behavioural data, empirical measurements are needed to determine the locations offshore where the birds spend most of their foraging effort. Radio-tagged chinstrap penguins followed by ship foraged a maximum of 8, 7.4, and 28 km from Seal Island in January 1989 and 22, 20, 24, 11 km from shore in January 1990 (Bengtson, personal observation). Combined with information from dive records, the tracking data suggest that chinstrap penguins nesting at Seal Island perform most of their foraging dives at a distance of about 3–25 km offshore.

Conclusions

During foraging trips to sea, chinstrap penguins from Seal Island made both shallow, short duration travelling dives (averaging 2.3 m and 10 s in depth and duration) and longer, deeper, U-shaped foraging dives (averaging 31.0 m and 71.3 s). Overall, foraging dives were relatively shallow and short in duration when compared to other penguins that have been studied. The birds adjusted their foraging behaviour to feed upon krill located for the most part within 50 m of the surface. Diving effort was highest during daylight, possibly due to the need for visual location of prey, chick provisioning, or perhaps to take advantage of diurnal changes in krill swarm densities or the behaviour of individual krill within the swarm. This observation contrasts with the hypotheses of Lishman & Croxall (1983), and Croxall *et al.* (1988) where it was speculated that foraging effort in chinstrap penguins was concentrated during the night. During foraging trips, chinstrap penguins at Seal Island dived almost continuously.

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¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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